

FIRST KNOWN SPECIMEN OF A HYBRID *BUTEO*: SWAINSON'S HAWK (*BUTEO SWAINSONI*) × ROUGH-LEGGED HAWK (*B. LAGOPUS*) FROM LOUISIANA

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ABSTRACT.—We report a specimen that appears to be a hybrid between Swainson's Hawk (*Buteo swainsoni*) and Rough-legged Hawk (*B. lagopus*), which, to our knowledge, is the first hybrid specimen for the genus. There are few reports of hybridization between *Buteo* species, most of which have been observations of inter-specific nesting pairs. The specimen described herein was collected in Louisiana and initially identified as a Rough-legged Hawk because of its feathered tarsi and the dark bellyband and carpals. A DNA sequence from the maternally inherited mitochondrial ND6 gene was identical to a published sequence for Swainson's Hawk. Nuclear DNA sequences from two introns contained only five variable sites among a panel of five potential parental taxa, but the hybrid sequence was most consistent with parentage by Rough-legged and Swainson's hawks. The feathered tarsi of the hybrid strongly suggested that the father was either a Rough-legged or Ferruginous hawk (*B. regalis*), the only North American raptors other than Golden Eagle (*Aquila chrysaetos*) that have feathered tarsi. Plumage and size characters were inconsistent with those of Ferruginous Hawk, and, other than the darkly pigmented leg feathers, were intermediate between the light morphs of Swainson's and Rough-legged hawks. The breeding range of Swainson's Hawk in Alaska and northern Canada is poorly known, but it overlaps that of the Rough-legged Hawk in at least a few locations, albeit at low densities, which may be a factor in hybridization. The occurrence of this hybrid is evidence of the potential for interbreeding between North American members of the genus *Buteo*, most of which are genetically closely related. Such hybridization could have implications for genetic diversity, adaptation, or the evolution of reproductive barriers. In any case, such hybrids present field and museum identification problems. Received 6 December 2004, accepted 3 October 2005.

Few documented cases of hybridization exist between any 2 of the 27 or so species in the genus *Buteo*. Hybrid combinations have been reported for Long-legged Buzzard (*B. rufinus*) and Upland Buzzard (*B. hemilasius*) in Asia (Pfander and Schmigalew 2001), Common Buzzard (*B. buteo*) and Long-legged Buzzard in Europe (Dudás et al. 1999), and Red-shouldered Hawk (*B. lineatus*) and Gray Hawk (*Asturina nitidus*) in North America (Lasley 1989). Additionally, an adult Swainson's Hawk (*B. swainsoni*) bred for more than 8 years with a presumably escaped South American Red-backed Hawk (Red-backed Buzzard, *B. polyosoma*) in Colorado, USA, and produced offspring in some years (Allen 1988, Wheeler 1988); a Red-tailed Hawk (*B. jamaicensis*) that escaped from a falconer bred with a Common Buzzard in Scotland (Murray 1970). However, to our knowledge, there are

no museum specimens of the offspring of such unions. Thus, it was with great interest that we found a specimen of an apparent hybrid in the Louisiana State University Museum of Natural Science (LSUMNS), Baton Rouge. It is a juvenile male, has feathered tarsi and mostly dark carpal patches, was collected near Baton Rouge, Louisiana, and was identified as a Rough-legged Hawk (*B. lagopus*). Its plumage appears almost the same as that of a probable hybrid between the same two species, first seen and photographed in November 2002 by Martin Reid near Ft. Worth, Texas; WSC observed and took photos of that bird in January 2003.

Herein we present a description of the putative hybrid *Buteo* based on its morphology, plumage, and mitochondrial and nuclear DNA sequences. A comparison of the hybrid to a set of potential parental *Buteo* taxa led to the conclusion that it descended from the mating of a female Swainson's Hawk with a male Rough-legged Hawk. Although not shown on some published range maps, Swainson's Hawks breed sparsely throughout at least a part of the Rough-legged Hawk's breeding range in far-northern North America.

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METHODS

WSC noted that the specimen, LSUMZ 159785, which was stored with a handful of juvenile light-morph Rough-legged Hawks, differed from them and was much like a presumed hybrid he had seen and photographed near Ft. Worth, Texas in January 2003. After a comparison of this specimen with those of juvenile Rough-legged and Swainson's hawks, he determined that it might be a hybrid. The specimen had been collected on 4 November 1994 in East Baton Rouge Parish, Highway 30 at Burtville, Louisiana, by S. W. Cardiff and D. L. Dittmann. A tissue sample was deposited in the LSUMNS Collection of Genetic Resources (catalog No. B23743). The specimen was sexed internally as a male (left testis 7×11 mm) and was in juvenal plumage; the skull was 75% ossified.

We used a DNEasy tissue kit (Qiagen, Valencia, California) to extract DNA from frozen muscle tissue of the putative hybrid specimen, and one specimen of each of the following taxa: Rough-legged Hawk, Swainson's Hawk, Red-tailed Hawk, Harlan's Red-tailed Hawk (*B. jamaicensis harlani*), and Ferruginous Hawk. We amplified the mitochondrial ND6 gene for the hybrid specimen in 25 μ l PCR reactions using Amplitaq Gold (Applied Biosystems [ABI], Foster City, California) with the primers tPROFwd and tGLUrev (Haring et al. 1999). For all six specimens, we amplified two nuclear loci, as follows: (1) intron 5 and flanking exon regions of the cytosolic adenylate kinase gene (AK1) using the primers AK5b+ and AK6c- (Shapiro and Dumbacher 2001), and (2) intron 3 and flanking exon regions of the Z-chromosome-linked muscle-specific receptor tyrosine kinase gene (MUSK) using primers designed by F. K. Barker: MUSK-E3F (CTTCCATGCACTAC AATGGGAAA) and MUSK-E4R (CTCTGA ACATTGTGGATCCTCAA). Standard PCR reactions were run on an MJ Research PTC-200 thermal-cycler under the following temperature regime: initial denaturation at 95°C for 8 min; 35 cycles of 92°C for 20 sec, 55°C for 60 sec, 72°C for 60 sec; and a final extension at 72°C for 10 min. For MUSK, the annealing temperature was adjusted to 50°C. Negative control reactions were used for all extractions and PCR to insure against contam-

ination. PCR products were purified using a Qiagen Gel Extraction Kit (Qiagen, Valencia, California). Cycle-sequencing reactions were carried out in both directions using the primers described above in quarter- or sixteenth-volume reactions with a Big Dye Terminator Cycle Sequencing Kit (ver. 2 or 3.1, ABI). Cycle-sequencing products were purified using Sephadex columns. Purified samples were electrophoresed on an ABI 377 or 3100 automated sequencer. Sequences were assembled and edited using Sequencher 4.2.2 (Gene Codes Corporation, Ann Arbor, Michigan). The ND6 sequence was compared with published sequences for various *Buteo* species (Riesing et al. 2003).

We compared morphology and plumage of the hybrid to a panel of five potential parental taxa. We followed the "contradictory characters" approach of Rohwer (1994) to eliminate potential pairs of parental taxa for which characters of the presumed hybrid fall outside of the range of variation. We assembled standard measurements of body mass, wing chord (unflattened), exposed culmen, and hallux (Baldwin et al. 1931) for juvenile males of potential paternal taxa from banding data for Swainson's, Rough-legged, and eastern Red-tailed hawks (*B. j. borealis*), and from museum specimen data for western Red-tailed (*B. j. calurus*), Harlan's Red-tailed, and Ferruginous hawks. We performed two stepwise discriminant function analyses with these four morphological variables using SPSS ver. 11.5 (SPSS, Inc. 2002). In both stepwise analyses, we used 0.05 probability of *F* for entry and 0.10 probability of *F* for removal of each variable, set equal prior probabilities of group membership, and used within-group covariance matrices. The three Ferruginous Hawk specimens were not included in the analysis due to small sample size, and the single Harlan's Red-tailed Hawk individual was included in the western Red-tailed Hawk group. The first discriminant function analysis included Rough-legged, Swainson's, eastern Red-tailed, and western Red-tailed hawks as groups. All four morphological variables were significant and included in the final model, and three significant discriminant functions were generated. The putative hybrid individual and the three Ferruginous Hawks were then classified using these discriminant functions. In the sec-

ond discriminant function analysis, we only included Rough-legged and Swainson's hawks as groups. Only mass, wing chord, and culmen were significant and included in the final model, and only one discriminant function explained 100% of the variation between the two groups. The putative hybrid was then again classified according to this discriminant function. To account for possible shrinkage of museum specimens relative to live birds (Winker 1993), we repeated all analyses under the assumption of a 3% reduction in size due to drying. The adjustment for shrinkage had no substantive effect on the results. Finally, with respect to plumage characters, we compared the specimen with juvenile male Swainson's and Rough-legged hawks, including pigmentation of the head, upperparts, breast, belly, tail, and legs, and emargination of the seventh primary (P7).

RESULTS

The mitochondrial DNA sequence of the putative hybrid, totaling 558 bp, was an identical match to a published sequence from a Swainson's Hawk collected in New Mexico (Table 1; GenBank accession No. AY213028). The sequence was 0.76% divergent from its nearest relative, the Galapagos Hawk (*B. galapagoensis*), and 3.23–3.58% divergent from the only sympatric congeners: Red-tailed, Ferruginous, and Rough-legged hawks (Clark and Wheeler 2001, Riesing et al. 2003; Table 1). Mitochondrial haplotypes are shared between mothers and their offspring because the mitochondrial genome is non-recombining and maternally inherited (Lansman et al. 1983). The identical mtDNA sequences of the specimen and a known Swainson's Hawk strongly suggests that the maternal parent was a Swainson's Hawk.

The nuclear AK1 sequence of the putative hybrid, totaling 542 bp, was identical to sequences from the Swainson's, Rough-legged, eastern Red-tailed, Harlan's, and Ferruginous hawks. The complete lack of variation at this locus prevents the elimination of any of these taxa as potential parents. The nuclear MUSK sequence, totaling 599 bp, contained five variable sites for the six taxa included in this study (Table 2). Among the five variable sites was a substitution unique to the Ferruginous Hawk sample (T; site no. 480), and another

TABLE 1. Uncorrected percent DNA sequence divergence between the presumed *Buteo* hybrid and potential parental *Buteo* taxa at mitochondrial (ND6) and nuclear (AK1 and MUSK) loci, with GenBank accession numbers. The mtDNA of the hybrid matches that of Swainson's Hawk, and the nuclear introns are most similar to those of Swainson's and Rough-legged hawks.

Species	Source	ND6 GenBank no.	ND6 % divergence from hybrid	AK1 GenBank no.	AK1 % divergence from hybrid	MUSK GenBank no.	MUSK % divergence from hybrid
Hybrid							
<i>B. swainsoni</i>	LSUMZ ^a B23743	DQ101251	—	DQ101247	—	DQ101254	—
<i>B. swainsoni</i>	Riesing et al. 2003	AY213028	0.00	—	—	—	—
<i>B. swainsoni</i>	LSUMZ B23587	—	—	DQ101248	0.00	DQ101257	0.00
<i>B. swainsoni</i>	Shapiro and Dumbacher 2001	—	—	AF307892	0.00	—	—
<i>B. lagopus</i>	Riesing et al. 2003	AY213017	3.23	—	—	—	—
<i>B. lagopus</i>	LSUMZ B8683	—	—	DQ101245	0.00	DQ101255	0.00
<i>B. lagopus</i>	Riesing et al. 2003	AY213018	3.58	—	—	—	—
<i>B. regalis</i>	LSUMZ B26245	—	—	DQ101249	0.00	DQ101255	0.17
<i>B. regalis</i>	Riesing et al. 2003	AY213019	3.23	—	—	—	—
<i>B. jamaicensis borealis</i>	LSUMZ B33264	—	—	DQ101250	0.00	DQ101253	0.17
<i>B. jamaicensis borealis</i>	LSUMZ B23470	—	—	DQ101246	0.00	DQ101252	0.17

^a Louisiana State University Museum of Natural Science, Baton Rouge.

TABLE 2. Variable sites on the 599 bp MUSK gene sequence for the presumed *Buteo* hybrid and five other buteos. The sites span part of exon 3, the entire intron 3, and part of exon 4, corresponding to positions 1311922–1312509 of the *Gallus gallus* chromosome Z genomic contig (GenBank NW 060751). Both states (i.e., A/T and A/G) are reported for heterozygous sites, as inferred by unambiguous double peaks on chromatograms.

	Variable position				
	65	113	157	452	480
Hybrid	A/T	A/G	C	A/G	C
Swainson's Hawk	T	A	C	G	C
Rough-legged Hawk	A/T	A/G	C	G	C
Ferruginous Hawk	T	A	C	G	T
Eastern Red-tailed Hawk	T	A	T	G	C
Harlan's Red-tailed Hawk	T	A	T	G	C

that was shared only by the eastern Red-tailed and Harlan's Red-tailed hawks (T; site no. 157). At two other sites (nos. 65 and 113), the Rough-legged Hawk and the hybrid were both heterozygous (A/T and A/G), with one exclusively shared state and one state in common with all other taxa (Table 2). The fifth variable site (no. 452) was heterozygous in the hybrid specimen only. Heterozygotes were inferred when chromatograms showed strong signal and unambiguous double peaks of nearly equal height.

We identified the paternal parent using phenotypic characters. Red-tailed Hawk, including Harlan's Hawk, can be eliminated as the putative father because it always has unfeathered tarsi. It seems unlikely that two species with bare tarsi would produce a hybrid with feathered tarsi. Further, the Red-tailed Hawk's culmen is considerably larger than that of the hybrid (Table 3). Finally, juvenile Red-tailed

Hawks share few plumage characters with the hybrid (Wheeler and Clark 1995, Clark and Wheeler 2001); we would not expect, for example, a hybrid Red-tailed Hawk \times Swainson's Hawk juvenile to have the heavy, dark bellyband (Fig. 1) or the dark carpal patches of the hybrid.

Both Ferruginous and Rough-legged hawks have feathered tarsi and are the most likely paternal candidates of the hybrid specimen. However, Ferruginous Hawks have noticeably wider gapes (Bechard and Schmutz 1995) and longer bills, wings, and halluces than the hybrid (Table 3). The measurements of the hybrid are far closer to those of Swainson's Hawk than to Ferruginous Hawk, suggesting that the bird is not intermediate in size as would be expected in an F1 hybrid between these two species. In contrast, the measurements for body mass and wing chord are intermediate between juvenile male Swainson's

TABLE 3. Comparison of measurements (mean \pm SE) of the hybrid *Buteo* specimen with juvenile male Rough-legged, Swainson's, Ferruginous, eastern Red-tailed, western Red-tailed, and Harlan's Red-tailed hawks. Body mass and wing chord of the hybrid are intermediate between Rough-legged and Swainson's hawks. Culmen and hallux are closest to Swainson's Hawk.

	<i>n</i>	Body mass (g)	Wing chord (mm)	Culmen (mm)	Hallux (mm)
Hybrid	1	702.0	381.0	19.3	21.4
Swainson's Hawk ^a	20	638.3 \pm 16.8	378.5 \pm 2.4	21.4 \pm 0.3	21.7 \pm 0.4
Rough-legged Hawk ^b	39	860.8 \pm 12.6	398.2 \pm 1.6	21.5 \pm 0.1	23.9 \pm 0.2
Ferruginous-Hawk ^c	3	1,091.4 \pm 14.3	413.7 \pm 1.8	25.0 \pm 0.3	25.6 \pm 0.3
Eastern Red-tailed Hawk ^d	24	825.4 \pm 15.8	351.8 \pm 1.9	27.2 \pm 0.2	24.1 \pm 0.2
Western Red-tailed Hawk ^e	12	905.5 \pm 30.3	374.4 \pm 2.9	24.2 \pm 0.3	27.7 \pm 0.4
Harlan's Red-tailed Hawk ^f	1	932.0	365.0	23.5	26.0

^a Unpublished banding data from Texas and New Jersey, sex determined by size.

^b Unpublished banding data from New York, sex determined by size.

^c MVZ (Museum of Vertebrate Zoology, University of California, Berkeley) specimen data from California.

^d Unpublished banding data from New Jersey, sex determined by size.

^e MVZ specimen data from British Columbia, California, Arizona, New Mexico, and Nevada.

^f MVZ specimen data from British Columbia.

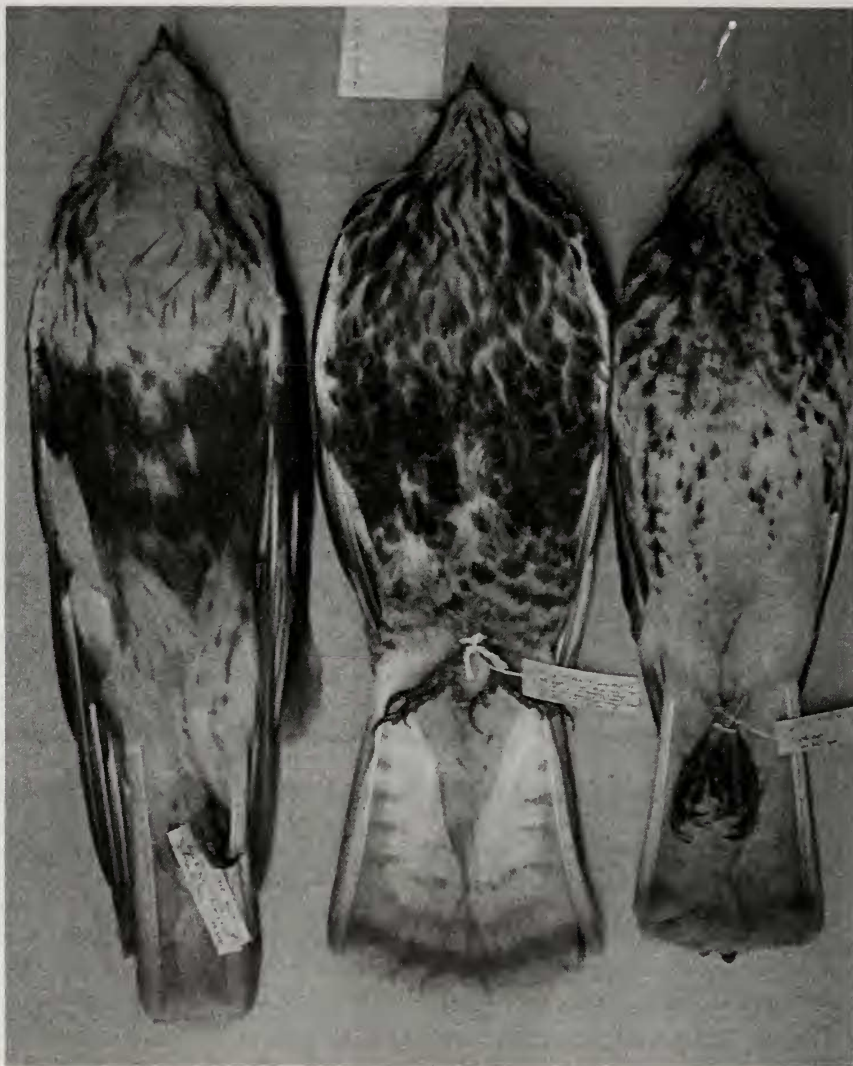


FIG. 1. Specimens showing ventral view of the hybrid *Buteo* (center), compared with juvenile male Rough-legged Hawk (left) and juvenile male Swainson's Hawk (right). Characters of the hybrid are intermediate.

and Rough-legged hawks (Table 3). Finally, the plumage characters of both light- and dark-morph juvenile Ferruginous Hawks do not match those of the specimen (Wheeler and Clark 1995, Clark and Wheeler 2001); a hybrid Ferruginous Hawk \times Swainson's Hawk juvenile, for example, would not be expected to have the dark bellyband (Fig. 1) nor the dark carpal patches of the hybrid.

Most plumage characters of the hybrid specimen are similar to those of juvenile male Swainson's or Rough-legged hawks, or intermediate between them (Figs. 1–2, Table 4).

The notching of P7 is also intermediate (Fig. 3). This feather has a noticeable abrupt widening or "notch" on the trailing edge for Rough-legged Hawk (same for Ferruginous and Red-tailed hawks) but not for Swainson's Hawk. The widening begins 93 mm from the tip on a juvenile male specimen Rough-legged Hawk (Fig. 3A), widening about 15 mm at an angle of 70° to the feather shaft. P7 on a juvenile male Swainson's Hawk specimen began widening gradually 47 mm from the tip and lacked a distinctive notch (Fig. 3B). The hybrid's P7 began widening 59 mm from the



FIG. 2. Specimens showing dorsal view of the hybrid *Buteo* (center), compared with juvenile male Rough-legged Hawk (left), and juvenile male Swainson's Hawk (right). Characters of the hybrid are intermediate.

tip with a notch and widened about 9 mm at a 60° angle (Fig. 3C).

In the first discriminant function analysis, which included Rough-legged, Swainson's, eastern Red-tailed, and western Red-tailed hawks as groups, the first two discriminant functions explained 96.2% of the variation between the groups (Fig. 4A). The first function correlated strongly with culmen ($r = 0.651$) and wing chord ($r = -0.513$) and explained 80.1% of the variance. The second function correlated strongly with hallux ($r = 0.814$) and body mass ($r = 0.646$) and explained

16.1% of the variance. Using both functions, the hybrid was classified as a Rough-legged Hawk with 31.2% probability, as a Swainson's Hawk with 68.8% probability, and as an eastern or western Red-tailed Hawk with 0% probability. In the second discriminant function analysis, which included only Rough-legged and Swainson's hawks as groups, one discriminant function explained 100% of the variation between the groups (Fig. 4B). This function correlated strongly with mass ($r = 0.875$) and wing chord ($r = -0.580$). Using this function, the hybrid was classified as a

TABLE 4. Comparison of plumage characters of the hybrid *Buteo* specimen with juvenile male Rough-legged and Swainson's hawks. Characters of the hybrid are intermediate or like one or the other of the parent species.

Character	Rough-legged Hawk	Swainson's Hawk	Hybrid
Crown	Pale	Dark	Dark, pale streaks
Superciliary	None	Rufous	Buffy
Malar	Narrow	Wide	Wide
Back feathers	Brown, pale sides	Dark brown, pale tips	Dark brown, pale tips and sides
Breast	Lightly streaked	Heavily streaked	Heavily streaked
Belly	Solidly dark	Buffy	Dark with pale edges
Legs	Feathered, lightly marked	Bare	Feathered, darkly marked
Uppertail	White base, dusky tip, no bands	Gray-brown, dark bands	Narrow white base, gray-brown, dark bands
Primary, outer web	Grayish cast	Dark	Grayish cast
Primary, inner web	Pale, no barring	Darker, barring	Pale, barring

Rough-legged Hawk with 45.4% probability and as a Swainson's Hawk with 54.5% probability.

DISCUSSION

Based on mtDNA, we conclude that the mother of this putative hybrid is a Swainson's Hawk. The most likely paternal candidates are raptors with feathered tarsi, Rough-legged and Ferruginous hawks. The latter was eliminated because of its plumage characters, much larger size, and unique MUSK intron haplotype.

Independent lines of evidence converged on the identification of the specimen as a hybrid between Swainson's and Rough-legged hawk. The combination of morphological and molecular characters, as in the diagnosis of a hybrid manakin (*Ilicura* × *Chiroxiphia*) by Ma-



FIG. 3. Notching of primary 7. (A) Rough-legged Hawk, (B) hybrid, and (C) Swainson's Hawk. The posterior margin of each P7 is highlighted in white. (Scale is not the same on each figure.) The shape of P7 of the hybrid is intermediate and unlike those of any *Buteo* species.

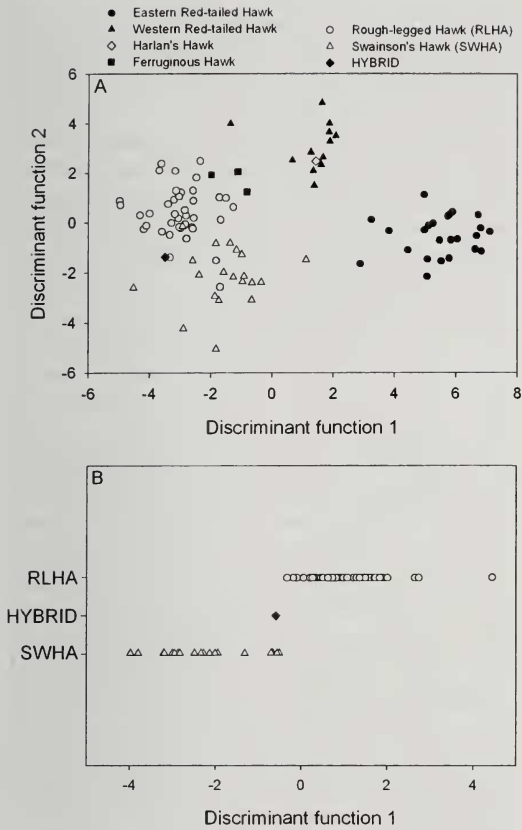


FIG. 4. Discriminant function analyses comparing juvenile males of *Buteo* species. In panel (A), plots of points along the first two significant discriminant functions are from an analysis that included Rough-legged, Swainson's, eastern Red-tailed, and western Red-tailed hawks as groups. These two discriminant functions explained 96.2% of the variation between the groups. The Harlan's Hawk was included in the western Red-tailed Hawk group, but was plotted with a unique symbol. The hybrid individual and three Ferruginous Hawks were then classified and plotted using these discriminant functions. In panel (B), points are plotted according to a discriminant function from an analysis that only included Rough-legged and Swainson's hawks as groups. One discriminant function explained 100% of the variation between the two groups. The hybrid was classified and plotted according to this discriminant function.

gests that its maternal parent was a Swainson's Hawk. The mother could have been a species other than Swainson's Hawk only if the mitochondrial identity were a mere artifact of incomplete lineage sorting. We consider this possibility unlikely because the mitochondrial study of Riesing et al. (2003) demonstrated that geographically heterogeneous samples of five Rough-legged, two Ferruginous, nine Red-tailed, and three Swainson's hawks are each reciprocally monophyletic, and the divergence levels between Swainson's Hawk and each of its sympatric congeners are greater than 3%.

The paucity of variation in the two nuclear introns illustrates the difficulty of using nuclear DNA to diagnose hybrids among closely related species. Intraspecific variation and lack of lineage sorting pose significant challenges to the conclusive identification of hybrid individuals, and these problems are compounded when potential parental taxa cannot be thoroughly sampled at the population level. Despite these difficulties, our sample of a single individual for each potential parental taxon yielded some variation that was consistent with the identification of Rough-legged Hawk as the paternal species. The eastern Red-tailed, Harlan's Red-tailed, and Ferruginous hawk samples each contained single substitutions on the MUSK intron that were not found in the hybrid. In contrast, only the Swainson's and Rough-legged hawk samples were completely compatible with parentage of the hybrid. Importantly, two heterozygous positions in the hybrid each contained a state that was shared exclusively with the Rough-legged Hawk sample.

Plumage and morphological characters of the hybrid specimen were generally intermediate between those of juvenile males of the parent species. This pattern is born out by the discriminant function analyses and is consistent with the characters of hybrids between other species of birds (e.g., Graves 1990, Rohwer 1994, Marini and Hackett 2002). However, the coloration of the tarsi feathers was not intermediate. Juvenile male Rough-legged Hawks have buffy tarsal feathers with sparse, dark markings, whereas Swainson's Hawks have bare tarsi. The hybrid specimen has tarsal feathers with heavy, dark barring, clearly not intermediate. The expectation that hybrid

rini and Hackett (2002), is a powerful method for the identification of avian hybrids. In particular, the comparison of a single mtDNA sequence to the growing database of published sequences is an outstanding tool for identification of the maternal parent. In this case, the mtDNA sequence of the hybrid strongly sug-

traits fall within the range of traits expressed by the parental taxa is based on the assumption that most traits are additive and polygenic (Falconer 1989) and is implicit in most hybrid diagnoses. Nonetheless, hybrids can also express traits that are extreme relative to those of the parental taxa (Rieseberg et al. 1999). It is possible that the darkly pigmented tarsal feathers could be one such transgressive trait, caused by complementary gene action, overdominance, or epistasis. Swainson's and Rough-legged hawk populations are known to possess genetic variation that results in differences in the quantity and distribution of melanin-based plumage pigments (Clark and Wheeler 2001). Rohwer (1994) reported other examples of characters that were not intermediate between those of the parental species. The culmen, and, to a lesser degree, the hallux of the hybrid were slightly smaller than our Swainson's and Rough-legged hawk measurements for those characters, providing another potential example of a non-intermediate character. However, specimen shrinkage could at least partly account for this difference.

The Swainson's Hawk breeds in an unknown amount of the breeding range of the Rough-legged Hawk in far northwestern North America. This is the extreme northern periphery of their distribution, and they occur at very low densities in taiga habitat where they are sympatric with the Rough-legged Hawk (England et al. 1997, Bechard and Swen 2002, Sinclair et al. 2003). This could increase the possibility that a female Swainson's Hawk could fail to find a conspecific mate. Given the broad overlap in distribution between Swainson's, Red-tailed, and Ferruginous hawks, the lack of documented instances of hybridization or interspecific pairings between any two of these three species suggests behavioral barriers to reproduction. Such barriers may not exist between Swainson's and Rough-legged hawks, which overlap only marginally and may have come into sympatry only recently. This hybrid pairing is consistent with the model of Short (1969), who proposed that hybridization is most likely to occur at the edges of a species' range.

Swainson's Hawks are rare during November in the area where the hybrid individual was found; there is only one November record for East Baton Rouge Parish, despite intensive

coverage by birdwatchers and collectors (LSUMNS data). Although Lowery (1974) indicated that Rough-legged Hawk is a regular winter visitor to Louisiana, and several subsequent sight-based reports lacking photos have been accepted by the Louisiana Bird Records Committee, the only physical evidence substantiating the occurrence of a Rough-legged Hawk in Louisiana is a specimen collected on 12 March 1933 at Grand Isle (LSUMZ 4803). The present hybrid occurred at a place (and time) unexpected for either species—Rough-legged Hawks should occur farther north and Swainson's Hawks farther south. This intermediate migratory behavior, as well as a myriad of other ecological differences between Swainson's and Rough-legged hawks, suggests potential sources of reduced fitness in hybrids. Hybridization can provide a mechanism for gene flow between species, particularly if hybrids are interfertile with parental species and do not suffer reduced fitness (Arnold 1992). Alternatively, hybrid unfitness can reinforce behavioral pre-mating barriers through natural selection (Saetre et al. 1997), particularly in taxa such as Swainson's and Rough-legged hawks that may have recently come into secondary contact.

Hybrids between raptor species are reported infrequently, most likely because they are rare, but also because they are difficult to diagnose in the field and are underrepresented in collections. That this specimen went unrecognized for 9 years after being collected underscores the field and museum identification problems posed by hybrids. Hybrids have been reported between Red Kite (*Milvus milvus*) and Black Kite (*M. migrans*) in Sweden (Sylvén 1977), a possible hybrid Rueppell's Vulture (*Gyps rueppellii*) and Cape Vulture (*G. coprotheres*) in Botswana (Borello 2001), Brown Goshawk (*Accipiter fasciatus*) and Grey Goshawk (*A. novaehollandiae*) in Australia (Olsen 1995), Shikra (*A. badius*) and Levant Sparrowhawk (*A. brevipes*) in Israel (Yosef et al. 2001), Pallid Harrier (*Circus macrourus*) and Montagu's Harrier (*C. pygargus*) in Finland (Forsman 1995), Western Marsh Harrier (*C. aeruginosus*) and Eastern Marsh Harrier (*C. spilonotus*) in Siberia (Fefelov 2001), and Greater Spotted Eagle (*Aquila clanga*) and Lesser Spotted Eagle (*A. pomarina*) in Latvia (Bergmanis et al. 1996). We

were unable to locate a copy of Suchelet (1897), who apparently reported a hybrid between Common Buzzard and Rough-legged Hawk. Most unusual were intergeneric hybrids reported between Black Kite and Common Buzzard near Rome, Italy, that produced rather strange-looking offspring (Corso and Glidi 1998). Equally unusual was a pairing between Gyrfalcon (*Falco rusticolus*) and Peregrine Falcon (*F. peregrinus*), in which both members of the pair were females (Gjershaug et al. 1998). The hybrid Turkey Vulture × Black Vulture reported by McIlhenny (1937) was later determined to be a practical joke (Jackson 1988). Most instances of hybridization listed above were determined at the nests by observing that the adults were different species, although one was a hybrid captured for banding (Yosef et al. 2001) and another was identified using field observations and photographs (Corso and Glidi 1998).

To our knowledge, our report is the first of a hybrid specimen arising from two *Buteo* species, and, perhaps, the first hybrid specimen for any raptor. It provides the first conclusive documentation of hybridization between two native North American members of the genus *Buteo*. A pairing of a Red-shouldered Hawk with a Gray Hawk (Lasley 1989) produced a downy chick, but it did not fledge, and there were neither photographs nor specimens from this union.

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